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Influence of deer, cattle grazing and timber harvest on plant species diversity in a longleaf pine bluestem ecosystem

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Abstract

Despite a recent slowing in the negative historical trend, losses of naturally-regenerated longleaf pine forests currently continue, largely as a result of conversion to plantations of faster growing pine species. Comparing the impacts of type conversion with silvicultural approaches that maintain longleaf pine and ascertaining their interaction with the influence of other resource management practices, such as grazing, on plant species diversity are essential in discerning the effects of these activities on the long-term sustainability of these ecosystems. A flatwoods longleaf pine bluestem ecosystem, which naturally regenerated following timber harvest during the early 20th century, on the coastal plain of southern Alabama was thinned to a residual basal area of 17 m²/ha or clearcut, windrowed and planted with slash pine (Pinus elliottii) seedlings in 1972 and then fenced in 1977 to differentially exclude grazing by deer and cattle. Neither grazing by deer alone nor deer in combination with cattle significantly altered vascular plant cover or species diversity; however, substantial differences were noted between the understory plant communities in the thinned forests and clearcut areas. Woody understory vegetation steadily increased through time, with woody plant cover in clearcuts (41%) dominated by the tree seedlings of Pinus elliottii and Quercus spp. being greater than that in thinned forests (31%) which were dominated by shrubs, principally Ilex glabra. While grass cover dominated by Schizachrium scoparium and Andropogon spp, remained stable (\sim 81%), the foliar cover of all forbs declined through time (from 42 to 18%) as woody plant cover increased. Although the overall species richness and diversity declined and evenness increased through time, understory species richness and diversity were consistently higher in thinned forests than in artificially-regenerated clearcuts. Despite a modest short-term decline in this differential, indicating a partial recovery of the clearcut areas over time, the disparity in understory plant diversity between thinned forests and clearcuts persisted for at least a decade. Whether grazing includes domestic cattle or is limited to native ungulates, such as white-tailed deer, we recommend that longleaf pine forests not be clearcut and replaced by plantations of other pines, if the ecological diversity is to be conserved, high quality habitat is to be maintained and longleaf pine ecosystems are to be sustained.

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1. Introduction

The once extensive longleaf pine (*Pinus palustris*) ecosystems of the southeastern US are well known for possessing high levels of species richness and much valued as high quality habitat for numerous wildlife

species (Stransky, 1971; Croker, 1987; Peet and Allard, 1993; Counts, 2000; Engstrom et al., 2001). The broad natural range of these ecosystems, spanning the physically diverse landscape of coastal plains from Texas through Florida to Virginia and piedmont and mountains into northern Alabama and Georgia, includes a wide variety of sites from wet flatwoods to xeric sandhills and rocky mountain ridges (Boyer, 1990; Stout and Marion, 1993). Naturally occurring as forests, woodlands and savannas, longleaf pine ecosystems are typically an uneven-aged mosaic of evenaged patches distributed across the landscape, which vary in size, shape, structure, composition and density and contain numerous embedded special habitats such as stream bottoms, wetlands and seeps (Platt and Rathbun, 1993; Brockway and Outcalt, 1998; Hilton, 1999). The natural variability of these ecosystems make them excellent habitat for popular game animals like white-tailed deer (Odocoileus virginianus), eastern wild turkey (Meleagris gallapavo), northern bobwhite quail (Colinus virginianus) and numerous nongame and rare animal species, including Sherman's fox squirrel (Sciurus niger shermani), southeastern pocket gopher (Geomys pinetis), Bachman's sparrow (Aimophila aestivalis), brown-headed nuthatch (Sitta pusilla), red-cockaded woodpecker (Picoides borealis), gopher tortoise (Gopherus polyphemus), eastern indigo snake (Drymarchon corais couperi), eastern diamondback rattlesnake (Crotalus adamanteus), flatwoods salamander (Ambystoma cingulatum) and others (Kantola and Humphrey, 1990; Engstrom, 1993; Guyer and Bailey, 1993; Crofton, 2001).

Since pre-settlement times, these vast forest ecosystems have steadily declined from \sim 38 to 1.2 million ha as a result of land clearing for agriculture, conversion to industrial plantations and interruption of natural fire regimes (Pyne, 1982; Wright and Bailey, 1982; Ewel, 1990; Frost, 1993). Excessive consumption of longleaf pine seedlings by feral hogs (Sus scrofa) also contributed to this loss, by seriously hindering the natural regeneration of many longleaf pine forests (Croker, 1987; Simberloff, 1993; McGuire, 2001). With these ecosystems now occupying only 3% of their original range (Means and Grow, 1985; Noss et al., 1995), habitat fragmentation and the increasing rarity of numerous plant and animal taxa (Hardin and White, 1989; Conner and Rudolph, 1991; Walker, 1993) have stimulated discussion concerning

how this negative trend can be reversed through ecological restoration (Myers, 1993; Brockway et al., 1998; Johnson and Gjerstad, 1998, 1999; Brockway and Outcalt, 2000; Holliday, 2001; Provencher et al., 2001) and the many resource values associated with longleaf pine forests can be sustainably managed (Landers et al., 1990, 1995).

To be successful, the sustainable management of longleaf pine ecosystems must provide opportunities to achieve stewardship goals, such as biological diversity conservation, and to use resources through activities such as timber harvest, pine-straw raking, livestock grazing and sale of hunting leases. Indeed, without consideration of economic benefits, conservation efforts are usually doomed to fail in the long-term (Kimmins, 1992; Oliver, 1992). Balancing economic development and biological diversity conservation is the major challenge currently facing forest management professionals (Aplet et al., 1993; Isik et al., 1997). A clear understanding of how modern land management practices affect the ecological resources of these fire-dependent and species-rich longleaf pine ecosystems is therefore essential.

Tree planting, thinning, harvesting, prescribed burning, selective application of herbicide and other silvicultural practices have profound influences on the longleaf pine forests and, when applied as individual or combination treatments, can contribute to the longterm sustainability of these ecosystems (Farrar, 1991, 1996; Brockway and Outcalt, 1998). Planting longleaf pine trees following harvest increases the diversity and abundance of breeding birds within 3-7 years (Hill, 1998a). Periodically burning and thinning longleaf pine improves habitat quality for quail and numerous other bird species and enhances the cover of grasses and forbs, thereby increasing the forage available to deer and cattle (Grelen and Enghardt, 1973; Hill, 1998b). Recurrent fire also benefits red-cockaded woodpecker populations by stimulating nutrient cycles and improving the dietary nutrition and the overall health of this rare species (James et al., 1997). Thinning longleaf pine stands typically increases herbaceous plant cover and density by increasing the light and soil water available to understory plants (Harrington and Edwards, 1999). Similar groundcover increases can be obtained when herbicide is used to selectively reduce competing hardwood trees and shrubs (Brockway et al., 1998). Livestock grazing

can also be a useful silvicultural technique that effectively controls understory vegetation, reducing the fire hazard without damaging pine seedlings (>2 years old) or increasing soil erosion and degrading surface water quality (Patric and Helvey, 1986; Pearson, 1987, Allen and Bartolome, 1989; Landers et al., 1990). The herbaecous plant understories of longleaf pine ecosystems have long served as an important forage resource, benefitting both deer and cattle (Halls et al., 1952; Lewis et al., 1974).

Deer are a major herbivore indigenous to many forest ecosystems. Although their diet principally consists of woody plants, hard mast and mushrooms, as much as 36% of their intake may be composed of forbs, grasses and sedges (Harlow, 1961; Harlow and Hooper, 1972; Hurst and Warren, 1981). While deer grazing normally has low to moderate impact on forest plants, damage done to plant communities by the heavy grazing of large deer populations is well documented (Ross et al., 1970; Marquis, 1981; Marquis and Brenneman, 1981; Cummins and Miller, 1982; Trumbull et al., 1989; Bergquist et al., 1999; Lawson et al., 1999). Common silvicultural practices directly or indirectly influence many aspects of deer habitat and food, including plant diversity, edge, distribution, availability, palatability, digestibility and nutrition (Halls and Boyd, 1982; Hurst and Warren, 1983; Hughes and Fahey, 1991; Ford et al., 1993, 1994; Johnson et al., 1995; Kilgo and Labisky, 1995; Thill and Morris, 1983; Thill et al., 1995; Peitz et al., 1999). Therefore, understanding the interactive influence of silvicultural practices and grazing by large ungulates on understory plant diversity in longleaf pine ecosystems is important for long-term sustainable management.

A longleaf pine bluestem ecosystem, that regenerated naturally following timber harvest in the early 20th century, was thinned or clearcut, windrowed and planted with slash pine (*Pinus elliottii*) seedlings and then fenced to differentially exclude grazing by deer and cattle. In measuring the post-treatment changes in the foliar cover, species diversity and standing biomass of vascular plants, the objectives of this study were to (1) evaluate the effects of deer grazing, cattle grazing and grazing exclusion on the understory plant community in forests harvested by clearcutting or thinning and (2) discern the rates of ecosystem change and recovery following these disturbances.

Comparative analysis should provide insights concerning the impacts of forest type conversion to slash pine and offer perspectives useful in developing management strategies for sustaining the ecological resource values of longleaf pine bluestem ecosystems.

2. Methods

2.1. Study site

This experiment was conducted on the Conecuh National Forest in Covington County, southcentral Alabama. The study site is located in the middle coastal plain physiographic province (Miller and Robinson, 1995) approximately 80 km north of the Gulf of Mexico (31°8′N,86°35′W), within the largest concentration of remaining longleaf pine forests (Outcalt and Sheffield, 1996). The climate is humid subtropical, with a 200-day growing season from April to October (NOAA, 1951–1978). Annual precipitation is abundant, averaging 1500 mm, with more than half of this arriving during the growing season (Cotton, 1989). Average monthly temperatures range from 18 to 27 °C for the April–October period and from 8 to 18 °C for November–March (NOAA, 1951–1978).

The study area is approximately 60 m above sea level in a flatwoods landscape consisting of broad, low, dry sandy ridges drained by shallow stream channels which flow slowly toward the Gulf of Mexico. Surface slopes, ranging from nearly level (0-2%) to gently inclined (<5%), are residuum derived from limestone. sandstone, siltstone and claystone dating from the Eocene to Oligocene ages (Turner and Scott, 1968). Soils developed in parent materials consisting of unconsolidated marine sediments, principally gravel, sand and clay. Predominant soils are the Orangeburg (Typic Paleudult, thermic), Troup (Grossarenic Paleudult, thermic), Dothan (Plinthic Paleudult, thermic), Bonifay (Grossarenic Plinthic Paleudult, thermic) and Fuquay (Arenic Plinthic Paleudult, thermic) series which are deep, well-drained loamy and sandy soils that are low in organic matter and nutrients and low to moderate in water holding capacity (Cotton, 1989).

Vegetation on this flatwoods area consisted of an overstory of longleaf pine growing in association with an understory rich in grasses, forbs, shrubs and vines (see Appendix A). Oak (*Quercus* spp.), cherry (*Prunus*

spp.), slash pine and longleaf pine were the predominant tree seedlings in the understory. Gallberry (*Ilex glabra*) was the most prominent shrub and splitbeard bluestem (*Andropogon ternarius*) and little bluestem (*Schizachrium scoparium*) dominated the graminoids. Scaleleaf aster (*Aster adnatus*), azure aster (*Aster azureus*), littleleaf tickclover (*Desmodium ciliare*), yankeeweed (*Eupatorium compositifolium*), goldaster (*Pityopsis* spp.), bracken fern (*Pteridium aquilinum*), coneflower (*Rudbeckia* spp.) and goldenrod (*Solidago* spp.) were the most commonly observed forbs.

2.2. Site history and experimental treatments

The study site was occupied by a second-growth longleaf pine forest that regenerated naturally following the harvest of old-growth longleaf pine during the early 20th century. Since early settlement of this area, low-intensity cattle grazing had been sporadically practiced. Prior to study initiation, the site had not been grazed by livestock for >40 years. In 1972, the maturing longleaf pine overstory was reduced by thinning to 17 m²/ha or eliminated by clearcutting. On the clearcut areas, logging slash was windrowed and, in winter 1973, slash pine seedlings were planted in rows using a $2.4 \,\mathrm{m} \times 3.7 \,\mathrm{m}$ spacing. As a typical prescription for converting longleaf pine to slash pine, this intensive site preparation treatment, which scraped away much of the topsoil, greatly disturbed the forest plant community.

In 1977, a randomized complete block experimental design was established on the study site. Three grazing treatments were replicated in three allotments distributed across the 2700 ha study area. Each 900 ha allotment contained six 150 ha blocks, three located within thinned forests and three in clearcut areas. To avoid the confounding influences of freely-moving cattle, the perimeter of each block was fenced with barbwire. Each 150 ha block contained three 0.1 ha $(23 \text{ m} \times 46 \text{ m})$ plots. Treatments were randomly assigned to plots within each block and consisted of (1) no grazing by deer or cattle, (2) grazing by deer and (3) grazing by deer and cattle. Deer and cattle exclusion was achieved by constructing an outrigger fence around the perimeter of each 0.1 ha plot (Jones and Longhurst, 1958; Messner et al., 1973). Cattle access was denied by installing a four-strand barbwire fence around the perimeter of each 0.1 ha plot. Plots grazed by both deer and cattle remained unfenced. Where not excluded by fencing, cattle grazing of moderately-low intensity occurred all year long at a rate that remained relatively constant during the study period. The established management practice for several decades of winter burning with prescribed fire at 3-year intervals was suspended across the entire area during the study.

2.3. Measurements

In September 1977, plant cover was measured on all study plots to ascertain the pre-treatment status of the understory plant community. Repeated post-treatment measurements were then completed in September and October 1978-1981 to assess the ecological changes resulting from differential grazing in both the thinned forests and clearcut areas. Total foliar cover (vertical projection of canopy) of all understory plant species was measured by line-intercept method along three permanent 20 m line transects within each treatment plot. Identification and nomenclature for plant species were consistent with taxonomic authorities (Clewell, 1985; Godfrey, 1988; Grimm and Kartesz, 1993; Wunderlin, 1998; Duncan and Duncan, 1999; Miller and Miller, 1999). Herbaceous biomass was measured on three randomly selected 1 m² sampling subplots within each of the larger treatment plots grazed by cattle and where cattle were excluded. Standing biomass of herbaceous plants was sampled by clipping at the groundline.

Herbaceous plant samples were dried to constant mass in a force draft oven at 70 °C for 24 h and weighed. These data were used to compute utilization rates of plant biomass by cattle. Foliar cover data for each species were summarized as estimates for each plot and analyzed by treatment and change through time. These data were then used as importance values to compute several diversity indices (Ludwig and Reynolds, 1988). Species richness (N_0) was characterized on each plot by counting the number of species present, evenness was calculated using the modified Hill ratio (E_5) and diversity was estimated using the Shannon diversity index (H'). Foliar cover data were then used as values of cumulative proportional abundance (CPA) to generate comparative diversity profiles which graphically illustrated the status of and change in plant community diversity through time (Swindel et al., 1987; Lewis et al., 1988).

All data for dependent variables were summarized as estimates of the mean for each experimental plot. Each plot mean was then used to estimate the mean and variance of each experimental treatment. For each dependent variable, a comparison of differences among experimental treatments and through the time sequence of repeated measurements was then undertaken. A repeated measures ANCOVA, using initial conditions as covariates, was used to evaluate time and treatment effects and interactions (Hintze, 1995). Responses of grazing treatments and timber harvest methods were compared using a set of five pairwise contrasts. The trend through time after treatment was analyzed using orthogonal polynomials. Statistical analysis of the time and treatment interaction for computed diversity indices was completed using the bootstrap technique PROC MULTTEST in SAS (Efron and Tibshirani, 1993; Westfall and Young, 1993; SAS Institute, 1996). Adjusted P-values, which maintain a constant type I error across the full range of comparisons, were used to determine significant differences among means (10,000 bootstrap iterations were used). A probability level of 0.05 was used to discern significant differences.

3. Results

3.1. Grazing effects

One decade following overstory reduction and four growing seasons after installation of the deer and cattle exclosures, no significant differences in foliar cover, plant species diversity or herbaceous biomass could be attributed to the grazing treatments. Despite a 41% forage utilization rate by cattle of the standing herbaceous biomass (558 \pm 10.1 kg/ha), comparisons with deer-grazed and ungrazed treatments indicated a minimal differential impact upon the understory plant community. Examination of data for each plant species showed that higher variation in foliar cover values was most frequently associated with the cattle grazing treatment. Although this greater variation may have contributed to these broadly non-significant findings, it is more likely that the differential grazing impact on the plant community was small because of the relatively light grazing intensity brought to bear by welldispersed ungulate populations.

3.2. Foliar cover

Although the total foliar cover of understory vascular plants remained relatively stable, woody plant cover increased significantly during the period of study (Table 1). The expanding cover of woody plants resulted primarily from significant increases in the cover of tree seedlings, principally slash pine and oaks, with minimal contributions from longleaf pine and other tree and shrub species. The understory cover of woody plants on plots where the overstory was clearcut and slash pine seedlings planted was significantly greater (a 4-year increase of 82%) than on those with a thinned overstory (18% increase). Growth of slash pine seedlings (and to a lesser extent, oak trees) in the clearcut areas accounted for this significant difference. While woody plant cover in clearcuts was dominated by tree seedlings, that in thinned forests was dominated by shrubs, primarily gallberry with lesser amounts of blackberry (Rubus spp.) and other species.

The collective cover of graminoids remained relatively stable, with only non-significant variation among treatments and through time (Table 1). However, splitbeard bluestem, the most abundant grass, increased significantly over time across all treatments (an average 4-year rise of 101%). Cover of little bluestem, the second most abundant grass, was significantly lower on clearcut areas than in thinned forests. No significant differences were observed in the numerous other graminoid species, which individually comprised a small proportion of this life form. By contrast, the total foliar cover of all forbs decreased significantly through time across all treatments. The rate of decline was somewhat greater for forbs growing in clearcut areas (a 4-year drop of 63%) than for those in thinned forests (50% decrease). Significant changes in the cover of Aster spp., Dioda teres, Polypremium procumbens, Rudbeckia spp. and Solidago spp. contributed to this trend.

3.3. Plant species diversity

The site supported a relatively rich plant community, with a total of 148 vascular plant species documented during the period of study. While 73 species of forbs were observed, these initially covered only 25% of the understory in the thinned forests and 59% in the

Table 1 Understory plant cover response to timber harvest and grazing (% foliar cover)

	Thinned overstory		Clearcut overstory			Adjusted	
	Ungrazed	Deer grazed	Cattle and deer grazed	Ungrazed	Deer grazed	Cattle and deer grazed	mean
All plants							
1977	148	136	149	177	175	192	
1978	129	138	111	145	156	172	127
1979	151	152	128	157	159	170	155
1980	161	160	128	160	168	199	162
1981	129	128	105	140	135	171	167
Adjusted mean ^a	151	165	127	139	145	189	
All woody plants							
1977	39.1	28.2	28.2	18.7	22.3	26.6	
1978	28.5	20.5	16.9	23.1	28.7	28.5	20.4
1979	33.5	27.0	21.9	38.1	38.7	34.3	32.5^{c}
1980	49.3	34.9	28.4	38.3	45.2	44.6	40.4^{c}
1981	50.4	35.4	27.0	38.2	45.7	38.9	37.9°
Adjusted mean	24.5	27.8	16.8	45.2 ^b	45.6 ^b	36.9 ^b	
Trees							
1977	4.4	4.7	15.3	10.7	11.9	12.7	
1978	2.1	3.5	6.9	15.8	16.0	17.1	5.0
1979	2.8	7.1	7.7	29.6	19.7	21.3	12.5°
1980	3.8	6.6	9.7	27.8	28.2	28.2	16.5°
1981	5.0	6.8	7.5	29.3	30.3	31.3	15.3°
Adjusted mean	12.3	13.8	11.0	23.1 ^b	21.2 ^b	24.5 ^b	
Longleaf pine							
1977	0.2	0.6	1.0	0.0	0.1	0.0	
1978	0.6	0.0	1.2	0.4	0.2	0.0	0.3
1979	0.5	0.2	1.5	0.3	0.4	0.1	0.6
1980	0.8	0.1	0.0	0.7	0.3	0.4	0.1
1981	1.1	1.1	1.9	0.2	0.0	1.7	0.7
Adjusted mean	0.8	0.2	1.2	0.4	0.2	0.5	
Slash pine							
1977	0.4	0.2	0.0	1.4	2.9	1.2	
1978	0.1	0.4	0.0	5.2	5.6	2.3	2.7
1979	0.0	0.1	0.0	9.7	7.7	3.1	4.7^{c}
1980	0.2	0.6	2.1	11.3	10.3	6.8	6.2^{c}
1981	0.0	0.0	0.0	13.7	12.4	11.2	5.9 ^c
Adjusted mean	1.2	1.6	2.6	9.5 ^b	6.5 ^b	3.8 ^b	
Oak							
1977	0.3	0.7	5.0	8.6	8.6	10.1	
1978	0.3	0.5	3.3	9.2	9.4	13.5	4.1
1979	0.4	1.2	3.1	17.4	15.2	16.1	8.5°
1980	0.8	1.0	4.7	13.7	16.4	18.2	10.8°
1981	1.0	0.4	3.0	13.2	17.7	16.1	11.2^{c}
Adjusted mean	9.0	8.5	4.3	7.6	9.4	8.2	
Shrubs and vines							
1977	34.7	23.5	12.9	8.0	10.4	13.9	
1978	26.5	17.1	10.0	7.3	12.7	11.5	15.7
1979	30.7	22.4	14.3	8.5	13.8	13.0	20.3
1980	45.4	28.4	18.7	10.5	17.0	16.4	24.3

Table 1 (Continued)

	Thinned overstory		Clearcut overstory			Adjusted	
	Ungrazed	Deer grazed	Cattle and deer grazed	Ungrazed	Deer grazed	Cattle and deer grazed	mean ^a
1981	45.4	28.7	19.5	8.8	15.5	7.6	22.9
Adjusted mean	19.7	18.7	20.9	18.5	21.9	25.2	
Gallberry							
1977	22.0	14.6	4.2	0.2	0.7	0.4	
1978	16.1	10.8	3.1	0.2	0.8	0.2	6.8
1979	20.7	15.1	4.2	0.0	0.6	0.4	8.6
1980	27.6	20.0	5.5	0.2	0.8	0.5	11.7
1981	30.9	15.3	5.4	0.2	1.0	0.6	9.7
Adjusted mean	8.5	4.0	1.7	2.9	3.5	4.5	
Blackberry							
1977	4.5	3.9	0.7	1.9	4.4	9.1	
1978	3.4	2.2	0.4	1.0	5.8	5.5	3.9
1979	2.7	1.7	1.3	1.3	5.1	2.3	5.4
1980	1.7	1.2	0.1	1.4	6.1	2.5	2.2
1981	3.7	1.0	0.0	1.0	5.3	4.1	3.3
Adjusted mean	2.3	1.7	4.1	2.3	5.5	6.3	
Graminoids							
1977	83.9	82.4	96.0	102.9	88.0	110.7	
1978	75.2	82.3	68.1	84.0	79.0	109.2	87.4
1979	96.4	98.3	83.7	83.1	75.5	108.4	105.5
1980	96.0	104.3	77.6	89.0	86.2	128.2	120.4
1981	68.8	77.8	65.0	84.1	61.4	111.6	118.3
Adjusted mean	82.5	87.8	30.4	87.2	84.6	115.0	
Splitbeard bluestem							
1977	12.3	14.1	0.7	3.9	1.2	7.5	
1978	12.4	21.2	0.6	9.9	4.1	13.1	11.0
1979	20.7	28.2	2.0	8.5	4.5	20.0	20.2°
1980	26.9	33.8	2.3	10.0	6.7	26.4	23.4°
1981	16.2	25.0	3.7	9.5	5.1	20.2	19.1°
Adjusted mean	13.0	14.7	6.0	27.4	24.4	18.2	
Little bluestem	~ .			2.2	4.0		
1977	7.4	12.2	17.5	3.2	4.3	5.5	0.0
1978	19.5 19.8	19.3 23.0	8.9	4.9	1.4	4.3	9.9 3.9
1979 1980	19.8 9.7	16.3	1.3 5.0	4.9 7.4	2.4 1.4	5.6 9.1	
1981	9.7 7.6	12.0	6.1	3.3	0.0	0.0	10.1 7.1
	14.1	15.6	11.3	3.3 4.9 ^b	1.3 ^b	0.0 0.7 ^b	7.1
Adjusted mean	14.1	15.0	11.5	4.9	1.3	0.7	
Wiregrass							
1977	0.0	0.5	0.0	0.0	0.0	0.0	
1978	0.3	0.5	0.0	0.0	0.0	0.0	0.1
1979	0.1	0.4	0.4	0.3	0.2	0.3	0.3
1980	0.2	0.6	0.0	0.1	0.0	0.3	0.1
1981	0.4	0.2	0.0	0.4	0.6	1.0	0.6
Adjusted mean	0.4	0.4	0.3	0.4	0.4	0.5	
Forbs							
1977	25.1	25.0	25.1	55.7	65.1	54.9	
1978	25.2	32.4	25.7	37.6	48.6	34.1	46.9
1979	21.1	24.3	22.8	35.6	44.7	27.4	44.5

Table 1 (Continued)

	Thinned overstory		Clearcut overstory			Adjusted	
	Ungrazed	Deer grazed	Cattle and deer grazed	Ungrazed		Cattle and deer grazed	mean ^a
1980	15.8	21.0	22.5	32.3	36.8	26.0	29.2°
1981	10.1	14.3	13.5	17.3	27.8	20.2	27.9^{c}
Adjusted mean	20.1	17.9	16.6	13.7	19.9	14.7	

^a Post-treatment mean adjusted by analysis of covariance.

clearcut areas, declining in 4 years to 13 and 22%, respectively. The 40 species of graminoids present on site were the dominant plant group, with a combined foliar cover ranging from 61 to 128%. The 25 species of shrubs and vines recorded here ranged from 24 to 31% cover of the understory in the thinned forests and 11 to 15% in the clearcut areas. Of the 10 tree species noted in the understory, oaks were the dominant naturally-occurring group. The prominence of slash pine on clearcut areas was solely the result of its being

planted following timber harvest. Naturally-regenerated longleaf pine seedlings were present at low levels (<2% cover) across the entire study site.

Although species richness (N_0) was unaffected by grazing treatments, a significant decline in the number of plant species occurred through time across all treatments (Table 2). Species richness in the understory of thinned forests decreased 44%, from 50 to 28 species, while that on clearcut areas dropped 39%, from 49 to 30 species on average. Most of the species

Table 2 Plant species richness, diversity and evenness responses to timber harvest and grazing

	Thinned overst	Thinned overstory			Clearcut overstory		
	Ungrazed	Deer grazed	Cattle and deer grazed	Ungrazed	Deer grazed	Cattle and deer grazed	
No. of species							
1977	48.3	50.3	51.5	50.0	44.5	53.0	
1978	42.3	43.3	41.0	32.0^{a}	37.3	41.5	
1979	46.0	47.5	39.5	37.3	56.5	39.0	
1980	38.3	41.5	40.5	39.0	38.0	44.5	
1981	27.0°	29.0^{a}	27.0°	30.3 ^a	29.3 ^a	31.5°	
Shannon index							
1977	2.85	2.93	2.97	2.83	2.67	2.85	
1978	2.88	2.85	2.84	2.49	2.44	2.61	
1979	2.72	2.74	2.64	2.57	2.58	2.73	
1980	2.55	2.66	2,74	2.62	2.60	2.66	
1981	2.37 ^a	2.54 ^a	2.43 ^a	2.38 ^a	2.29 ^a	2.49	
Modified Hill ra	tio						
1977	0.61	0.67	0.59	0.53	0.55	0.59	
1978	0.69	0.66	0.70	0.59	0.55	0.62	
1979	0.59	0.61	0.60	0.63	0.57	0.68	
1980	0.62	0.62	0.72	0.67	0.64	0.67	
1981	0.67	0.71	0.67	0.71	0.67	0.70	

 $^{^{\}rm a}$ Significant decrease through time from 1977 pre-treatment condition, P < 0.05.

^b Significantly different from other treatments, P < 0.05.

^c Significant change through time from 1977 pre-treatment condition, P < 0.05.

lost were forbs which disappeared as woody plants (principally tree seedlings in clearcut areas) and splitbeard bluestem progressively increased their understory dominance. Plant species diversity, though not consistently significant, followed a similar declining trend through time. Values for the Shannon diversity index (H') decreased in thinned forests from 2.92 to 2.45 and on clearcut areas from 2.78 to 2.39 during the period of study. Values for species evenness were indicative of moderate equity in the distribution of plant species present on site. A small progressive increase through time in the modified Hill ratio (E_5) was noted across all treatments; however, this trend was not statistically significant. Therefore, diversity fluctuations were driven primarily by variations in species richness.

When CPA data for the 5-year period were plotted in a comparative diversity profile, the downward displacement of the curves from the unity line (y = x)indicated that the understory plant community in the thinned forests, displayed on the y-axis, contained greater species diversity than that in the clearcut areas, on the x-axis (Fig. 1). Over the study period, a pattern of increasing floristic convergence between the two communities is reflected by annual oscillations in proportional abundance which approach the unity line. As might be expected, the pattern of oscillations is not uniform across all species. Among the very common species (dominant grasses, x = 0-0.3), the pattern is one of divergence, followed by convergence, then continued convergence and divergence once again. Among the common species (prominent tree seedlings and shrubs: oaks, slash pine, gallberry, x = 0.3-0.65), the pattern is one of alternating years of convergence, divergence, convergence and divergence. The magnitude of these annual oscillations appears greatest in this group of plants. However, the less common and rare species (all other tree, shrub, graminoid and forb species, x > 0.65) seem to generally follow a pattern of annual oscillation like that of the very common

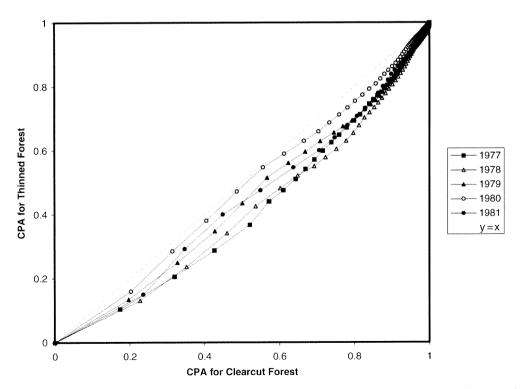


Fig. 1. Diversity profile comparing CPA in understory plant communities of thinned longleaf pine forests with those that were clearcut, site prepared and planted with slash pine.

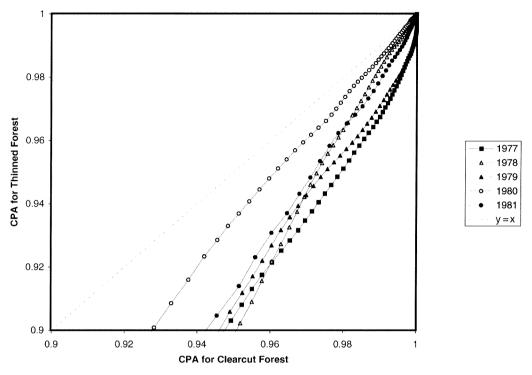


Fig. 2. Diversity profile comparing CPA of rare plant species in thinned longleaf pine forests with those in clearcuts.

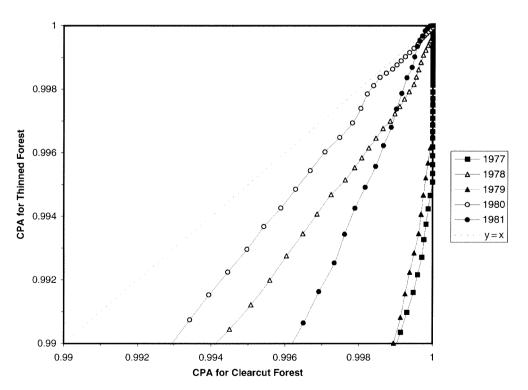


Fig. 3. Diversity profile comparing CPA of very rare plant species in thinned longleaf pine forests with those in clearcuts.

species, except with substantially more year-to-year variation.

Since ecosystem status is often judged by the presence and dynamics of the rarest species, data from the upper right-hand corner of Fig. 1, was displayed under $10 \times$ magnification for rare species in Fig. 2 and $100 \times$ magnification for very rare species in Fig. 3 to allow closer examination. The species represented in this region of the profile are almost exclusively forbs. While annual oscillations among rare species (x > 0.9) initially showed a pattern of convergence between the understory plant communities of the thinned forests and clearcut areas, much of this movement was negated by a substantial divergence trend during the 1981 growing season (Fig. 2). A similar pattern was present among the very rare species (x > 0.99), except that the annual fluctuations of convergence and divergence alternated with proportionally greater amplitude (Fig. 3). Although the two understory communities were quite divergent in 1977, substantial convergence occurred during the 1978, 1980 and 1981 growing seasons. This convergence trend was most pronounced among the extremely rare species (x > 0.999), which intersected or closely approximated the unity line in 1980 and 1981. While the understories of the thinned forests and clearcut areas remained distinctly different nearly a decade following harvest, largely because of intensive site preparation and the abundance of slash pine planted in clearcuts, the greatest degree of convergence between them appeared first among the extremely rare plant species.

4. Discussion

4.1. Grazing relationships

Neither grazing by deer nor cattle significantly altered the cover, diversity or biomass of the understory plant communities in this longleaf pine bluestem ecosystem. Since the deer population in this locale was known to be very high, averaging 14 deer/km² (Ken Johnson, Alabama Department of Wildlife and Freshwater Fisheries, personal communication), these results were initially puzzling. However, deer often avoid areas where cattle are actively grazing and, with consumption by cattle somewhat low, the forage

available to deer was not scarce. Thus, there was little incentive here for deer to jump fences to obtain food. Also, studies elsewhere in southern forests indicate that consumption rates as low as 2-3% are not uncommon and may be the result of deer food preferences and seasonal use patterns relative to a particular site (Harlow and Hooper, 1972; Johnson et al., 1995; Castleberry et al., 1999). Although cattle utilized about 41% of the forage available each year, their principal impact was on grasses that predominated in the understory and rapidly regrew in the abundant rainfall of this environment. Grasses, with their substantial nutrient stores in extensive belowground root systems and leaf meristems at least 4 cm below the ground surface, are readily adapted to survive grazing and other short-term disturbances (Lemon, 1949). Both temporal and spatial dispersion of ungulate populations likely contributed to this minimal differential effect.

4.2. Foliar cover changes

Complete canopy removal by clearcutting initiated more pronounced changes in the understory plant community than did forest thinning to a residual basal area of 17 m²/ha. The sudden increase in solar radiation reaching the understory and higher levels of available soil moisture stimulated increased growth of oaks already established in the clearcuts. A similar pattern was observed for planted slash pine seedlings which, together with the oaks, continued a rapid cover expansion that resulted in their domination of the developing overstory on clearcut areas. Grasses continued to dominate the understory, with the progressive expansion of splitbeard bluestem and a corresponding decrease in the cover of little bluestem. The rapid decline of forb cover was very likely a direct result of resource competition with the expanding canopy of developing slash pine and oaks. As ecological succession continues, this young forest will reach stand closure during the stem exclusion stage (aggradation phase), with the understory plant community further reduced and eventually transformed into a suite of largely shade-tolerant species (Bormann and Likens, 1979). An off-site slash pine forest will ultimately replace the former longleaf pine forest on the clearcut and planted areas.

By contrast, a substantial portion of the longleaf pine overstory was retained in areas receiving the thinning treatment. With the fundamental components of the forest intact, the understory plant community continued to be dominated by grasses, with gallberry and blackberry as the most prominent shrubs and longleaf pine and oak as the most prominent tree seedlings. Although forb cover also declined in these thinned forests, initial levels were lower than in the clearcuts resulting in decreases that were correspondingly less dramatic. The drop in forb cover may have been related to the progressive regrowth of the pine canopy, a commonly observed phenomenon in many forest types subsequent to overstory thinning (Miller, 1981; Bennett and Jones, 1983; Baker et al., 1996; Farrar, 1996; Schultz, 1997), and, to some degree, the expansion of splitbeard bluestem. Although increases in the cover of grasses and forbs are typically initial responses of longleaf pine overstory thinning (Harrington and Edwards, 1999), these increments may be short-lived as further stand development alters the patterns of sunlight and soil moisture availability and the amount of pine needle fall and forest litter accumulation in the understory.

4.3. Diversity dynamics

The 148 species of vascular plants present on the study site were clearly indicative of the high levels of species richness characteristic of longleaf pine ecosystems (Peet and Allard, 1993). As is typical of periodically burned longleaf pine flatwoods ecosystems, grasses dominated the understory plant community, with forbs, shrubs and tree seedlings occurring in substantial abundance. With 10 species of trees, 25 species of shrubs and vines, 40 species of graminoids and 73 species of forbs, this richness was well distributed among major plant groups. Plant diversity is largely determined by interspecific competition interacting with site productivity, microsite heterogeneity and disturbance regimes (Tilman, 1982). Herbaceous plant diversity is reported to initially increase and subsequently decline to predisturbance levels on sites impacted by prescribed fire, tree harvest or site preparation (Swindel et al., 1984). The two contrasting tree harvest methods examined in this study, thinning versus clearcutting followed by site preparation and planting, were expected to cause differential mortality among plant groups, altered competitive relationships among species and thus influence plant diversity dynamics.

The minimal differences in understory plant species richness, diversity and evenness between thinned forests and those that were clearcut, site prepared and planted with slash pine seedlings were indeed surprising. While some studies have reported no significant difference in the species richness between natural longleaf pine forests and plantations (Mejeur et al., 2000), plant species diversity is typically observed to increase following less intensive practices and decrease or remain unchanged after more intensive practices (Swindel et al., 1983; Elliott et al., 1997). Land use history has also been shown to have an important influence upon the understory plant community, particularly as related to agricultural uses (Hedman et al., 2000). Thus, the similar land use history of all plots on the study site may have in part accounted for the similar response to treatments. The most profound change in the understory plant community was a progressive decline in species richness across all treatments. This downward trend persisted through time and became statistically significant by the fourth post-treatment growing season. Although evenness among species demonstrated a modest nonsignificant increase over time, indicating a minor improvement in resource distribution equity among understory species, this effect was unable to offset the major negative impact of species loss upon plant diversity. As the canopy expanded on thinned plots and woody plants again asserted dominance on clearcut plots, understory plant diversity precipitously declined. This trend is likely to continue until each of these forests reaches a stage beyond stand closure that allows increased levels of light to reach the forest

Despite the unremarkable results among treatments observed from metrics commonly employed to quantify alpha diversity (N_0 , H' and E_5), CPA data arrayed in comparative diversity profiles clearly demonstrated that diversity levels in thinned forests consistently exceeded those in clearcut areas throughout the period of study. Not only is this difference reflected in the diversity profile for common plants, but also in those for rare and very rare plant species. The greatest

diversity difference between these two communities was noted following the initial disturbances. During the years that followed, a somewhat erratic, short-term convergence trend in the flora of these plant communities was observed across all plant species groups, as a period of recovery ensued. While common plants in the clearcut areas demonstrated the largest magnitude of recovery, rare plants and especially very rare species exhibited the greatest proportional recovery. Several of these very rare species, that were temporarily eliminated by harvesting disturbance, reappeared within the decade and recovered fully to achieve parity in abundance with levels measured in the thinned forests. These findings were similar to those reported in the flatwoods communities of northern Florida, where site disturbance and an initial reduction in common species allowed reappearance (usually in small quantities) of native, earlysuccessional species, especially forbs and grasses (Swindel et al., 1984). While such changes may at first appear to be introductions of new species, there was in fact no major invasion of new plants and the increase in diversity was the result of transferring abundance among the existing plant species (Lewis et al., 1988).

4.4. Sustaining the ecosystem

Prior to European contact, longleaf pine forests were among the largest ecosystems on the North American continent (Schwarz, 1907; Wahlenberg, 1946; Landers et al., 1995). However, the steady decline of these forests, resulting from land clearing, conversion to plantations of slash pine and loblolly pine, decreased frequency of periodic surface fires and seedling damage by feral hogs, has seriously jeopardized the long-term viability of longleaf pine ecosystems and the many species dependent upon them for habitat (Ewel, 1990; Frost, 1993; Harcombe et al., 1993; Noss et al., 1995, Conner et al., 2001). Efforts to reverse this downward trend have focused on developing various approaches for ecologically restoring and effectively managing longleaf pine forests to achieve long-term sustainability of numerous resource values (Croker, 1987; Landers et al., 1990; Boyer and White, 1990; Farrar, 1991; Boyer, 1993; Myers, 1993; Farrar, 1996; Brockway and Outcalt, 1998; Brockway et al., 1998; Johnson and Gjerstad, 1998, 1999; Brockway and Outcalt, 2000; Glitzenstein et al., 2001; Provencher et al., 2001).

Periodically thinning the overstory of longleaf pine forests, especially when done in combination with recurrent fire, is known to increase herbaceous plant growth and improve habitat quality for many wildlife species, including white-tailed deer, bobwhite quail, wild turkey and a variety of nongame species (Grelen and Enghardt, 1973; Harlow et al., 1980; Thill et al., 1987, 1995; Thill and Martin, 1989; Farrar, 1991; Haywood et al., 2001). Although cattle can reduce levels of grassy fuel (potentially diminishing the effectiveness of prescribed fire) and damage young longleaf pine trees under 3 m tall, a moderate level of grazing may also be compatible with achieving ecosystem sustainability objectives, as long as it is closely monitored and strictly controlled (Farrar, 1991). However, converting longleaf pine forests to other species (e.g. slash pine), not only contributes to the further attrition of these highly endangered ecosystems, but also replaces longleaf pine with overstory species that will drive community succession along a very different trajectory. Such fundamental change is highly likely to alter ecological processes (i.e. fire regime, regeneration dynamics) and forest stand structure, which will result in habitat degradation and loss of diversity among breeding birds and other species (Hill, 1998b). Therefore, regardless of whether grazing management includes domestic cattle or is limited to native ungulates, such as white-tailed deer, we recommend that natural longleaf pine forests not be clearcut and replaced by plantations of other pine species, if ecological diversity is to be conserved, high quality habitat for numerous wildlife species is to be maintained and longleaf pine ecosystems are to be sustained.

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Appendix A

Mean frequency of vascular plants on the Conecuh NF study site (% of plots where each species was observed along transects during the 5-year study period).

Scientific name	Common name	Overstory	
,		Thinned	Clearcu
Trees			
Carya tomentosa	Mockernut hickory	2	13
Cornus florida	Flowering dogwood	73	9
Diospyros virginiana	Common persimmon	22	64
Nyssa sylvatica	Black tupelo	13	0
Persea borbonia	Redbay	2	0
Pinus elliottii	Slash pine	31	98
Pinus palustris	Longleaf pine	36	31
Pinus taeda	Loblolly pine	0	11
Prunus spp.	Cherry	31	7
Quercus spp.	Oak	67	89
Shrubs and vines			
Asimina trilobata	Pawpaw	7	13
Calicarpa americana	American beautyberry	4	13
Campsis radicans	Trumpet-vine	4	2
Chrysobalanus oblongifolius	Cocoa-plum	7	31
Clethra alnifolia	Sweet pepperbush	9	0
Gaylussacia bacata	Black huckleberry	9	7
Gaylussacia dumosa	Dwarf huckleberry	67	96
Gelsemium sempervirens	Yellow jessamine	47	44
Ilex coriacea	Large gallberry	7	0
Ilex glabra	Gallberry	100	44
Ilex opaca	American holly	4	0
Ilex vomitoria	Yaupon holly	60	64
Myrica cerifera	Wax myrtle	73	29
Opuntia spp.	Prickly pear	0	9
Parthenocissus quinquefolia	Virginia creeper	0	7
Pyrus arbutifolia	Red chokeberry	11	2
Rhus copallina	Winged sumac	24	31
Rhus glabra	Smooth sumac	7	11
Rubus spp.	Blackberry	89	98
Schrankia spp.	Sensitive briar	4	2
Smilax spp.	Greenbrier	58	29
Toxicodendron radicans	Poison ivy	9	4
Toxicodendron toxicarium	Eastern poison ivy	11	2
Vaccinium myrsinites	Shiny blueberry	73	20
Vitis spp.	Grape	13	9
Graminoids			
Andropogon gyrans	Bluestem	36	49

Appendix A. (Continued)

Scientific name	Common name	Overstory		
		Thinned	Clearcut	
Andropogon tener	Slender bluestem	0	9	
Andropogon ternarius	Splitbeard bluestem	96	91	
Andropogon virginicus	Broomsedge bluestem	100	98	
Anthaenantia villosa	Green silkyscale	11	11	
Aristida beyrichiana	Wiregrass	33	29	
Aristida lanosa	Woolysheath threeawn	27	24	
Aristida longespica	Slimspike threeawn	24	62	
Aristida purpurescens	Arrowfeather threeawn	96	100	
Aristida spiciformis	Bottlebrush threeawn	2	7	
Aristida virgata	Trinius threeawn	11	9	
Axonopus affinis	Common carpetgrass	49	31	
Axonopus furcatus	Big carpetgrass	2	9	
Ctenium aromaticum	Toothachegrass	71	2	
Digitaria sanguinalis	Hairy crabgrass	7	22	
Eragrostis elliottii	Elliott lovegrass	9	0	
Eragrostis refracta	Coastal lovegrass	60	100	
Eragrostis spectabilis	Purple lovegrass	51	42	
Eustachys floridana	Windmillgrass	0	2	
Fimbristylus puberula	Hairy fimbry	56	96	
Gymnopogon ambiguus	Bearded skeletongrass	82	40	
Leptoloma cognatum	Fall witchgrass	7	7	
Muhlenbergia expansa	Cutover muhly	67	27	
Panicum spp.	Panic grass	100	100	
Panicum anceps	Beaked panicum	2	0	
Panicum verrucosum	Warty panicum	31	9	
Panicum virgatum	Switchgrass	27	4	
Paspalum floridanum	Florida paspalum	67	93	
Paspalum notatum	Bahiagrass	0	20	
Paspalum setaceum	Thin paspalum	0	4	
Rhynchospora spp.	Beakrush	22	20	
Schizachyrium scoparium	Little bluestem	80	71	
Scleria spp.	Nutgrass	51	40	
Sorghastrum elliottii	Slender Indiangrass	7	7	
Sorghastrum nutans	Yellow Indiangrass	31	27	
Sorghastrum secundum	Lopsided Indiangrass	36	69	
Sporobolus curtissii	Curtiss dropseed	4	2	
Sporobolus junceus	Pineywoods dropseed	36	58	
Tridens carolinianus	Carolina tridens	11	7	
Triplasis americana	Perennial sandgrass	11	18	
Forbs	C			
Agalinus setacea	Figwort	27	9	
Ambrosia artemisiifolia	Common ragweed	2	0	
Angelica spp.	Angelica	7	Ö	

Appendix A. (Continued)

Scientific name	Common name	Overstory	
		Thinned	Clearcu
Asclepias spp.	Milkweed	0	2
Aster adnatus	Scaleleaf aster	76	69
Aster azureus	Azure aster	71	53
Aster linariifolius	Savoryleaf aster	24	11
Baptisia spp.	Wild indigo	9	2
Bigelowia nudata	Yellowhead	7	0
Carphephorus bellidifolius	Chaffhead	4	4
Carphephorus odoratissimus	Vanilla plant	38	40
Cassia nictitans	Wild sensitive plant	40	58
Centrosema virginianum	Butterfly-pea	7	0
Chaptalia tomentosa	Pineland daisy	27	4
Cirsium spp.	Thistle	2	0
Clitoria mariana	Atlantic pigeonwings	2	2
Coreopsis leavenworthii	Leavenworth's tickseed	7	0
Croatalaria spp.	Rattlebox	4	9
Croton spp.	Croton	2	0
Desmodium ciliare	Littleleaf tickclover	71	67
Diodia teres	Poor joe	2	42
Dyschoriste spp.	Twinflower	2	4
Elephantopus tomentosa	Elephant's-foot	31	40
Erigeron vernus	Whitetop fleabane	7	7
Eriogonum tomentosum	Wild buckwheat	18	58
Eryngium yuccafolium	Button snakeroot	29	7
Eupatorium album	White thoroughwort	56	33
Eupatorium capillifolium	Dogfennel	11	9
Eupatorium compositifolium	Yankeeweed	78	80
Eupatorium mohrii	Mohr's thoroughwort	16	0
Eupatorium rugosum	White snakeroot	64	4
Euphorbia corrollata	Floweringspurge	24	16
Galactia spp.	Milkpea	27	27
Gaura filipes	Slenderstalk beeblossom	7	2
Gnaphalium spp.	Cudweed	20	36
Gratiola pilosa	Shaggy hedgehyssop	2	0
Habenaria quinqueseta	Longhorn false reinorchid	4	0
Helianthus spp.	Sunflower	67	29
Hibiscus aculeatus	Rough rosemallow	13	4
Hypericum crux-andraeae	St. Peter's-wort	11	9
Hypericum gentianoides	Pineweed	22	73
Hypericum tetrapelatum	Fourpetal St. John's-wort	0	2
Hyptis alata	Musky mint	18	7
Ipomea spp.	Morning-glory	13	44
Leachea torreyi	Pinweed	4	18
Lespedeza bicolor	Shrubby lespedeza	16	16

Appendix A. (Continued)

Scientific name	Common name	Overstory		
		Thinned	Clearcut	
Lespedeza capitata	Dusty clover	18	13	
Liatris spp.	Gayfeather	16	36	
Lobelia puberula	Downy lobelia	11	2	
Oxalis stricta	Yellow wood sorrel	62	27	
Piloblephis rigida	Pennyroyal	4	2	
Pityopsis spp.	Goldaster	100	98	
Polygala lutea	Bachelor's button	2	0	
Polygala nana	Candyweed	0	7	
Polypremium procumbens	Rustweed	7	76	
Pteridium aquilinum	Brackenfern	89	73	
Pterocaulon virgatum	Blackroot	13	11	
Rhexia spp.	Meadow beauty	20	7	
Rhynchosia spp.	Dollarweed	2	13	
Richardia scabra	Florida pusley	31	42	
Rudbeckia spp.	Coneflower	89	44	
Ruellia spp.	Wild petunia	4	0	
Scutellaria spp.	Skullcap	24	7	
Senecio spp.	Butterweed	2	0	
Silphium compositum	Rosin-weed	24	0	
Solidago spp.	Goldenrod	78	93	
Stylosanthes biflora	Pencilflower	20	2	
Tephrosia spp.	Hoarypea	27	38	
Tragia spp.	Noseburn	20	13	
Urtica chamaedryoides	Stinging nettle	27	13	
Veronica anagallis-aquatica	Water speedwell	11	22	
Viola spp.	Violet	27	22	
Xyris caroliniana	Yellow-eyed grass	2	0	

Total plant species = 148.

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